

EARLY AVIAN EVOLUTION IN THE SOUTHERN HEMISPHERE: THE FOSSIL RECORD OF BIRDS IN THE MESOZOIC OF GONDWANA

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The record of Gondwanan Mesozoic birds, including osteological specimens, feathers and traces, is critically reviewed. Data regarding the paleoenvironment and associated biota of each record is provided. Several occurrences of controversial status in the Late Triassic-Early Jurassic of Africa and the Cretaceous of Australia and Africa, and misguided reports from the Cretaceous of South America are also discussed. The Mesozoic record of Gondwanan birds is limited, although it has provided relevant insights about the early evolution of birds. Undisputable records are known from the Cretaceous of South America, Australia, Africa and Antarctica. This material indicates that during the Cretaceous, Gondwanan birds were widely distributed, inhabiting a broad range of environments and developing various modes of life. □ *Birds, Mesozoic, Gondwana, evolution.*

Se revisa críticamente el registro Mesozoico de avcs de Gondwana, incluyendo restos óseos, plumas y trazas. Para cada registro, se provee información con respecto al paleoambiente y la fauna asociada. Se discuten varios registros de status controvertido en el Triásico Tardío-Jurásico Temprano de Africa, y el Cretacico de Australia y Africa, como también reportes erroneos del Cretácico de América del Sur. El registro Mesozoico de aves de Gondwana es limitado, si bien ha provisto información relevante sobre la temprana evolución de las aves. Registros confiables son conocidos del Cretácico de América del Sur, Australia, Africa y Antártida. Este material indica que durante el Cretácico las aves de Gondwana estuvieron extensamente distribuidas, habitando un amplio espectro de ambientes y desarrollando diversos estilos de vida.

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The early evolutionary history of birds has been reconstructed mostly on the basis of fossil evidence provided by Mesozoic deposits of the northern hemisphere. It is not until recently that significant discoveries of Mesozoic birds from Gondwana have been made, and that this new evidence has strongly influenced our previous conceptions of avian evolution (Chiappe, 1995a).

The indisputable record of Mesozoic birds in Gondwana is restricted to the Cretaceous, although bird-like footprints have been found in pre-Cretaceous deposits. Among today's Gondwanan continental masses, South America, Antarctica, Australia and Africa have provided Cretaceous evidence of birds. The South American (Chiappe, 1991) and Australian (Vickers-Rich, 1991) records have been previously discussed elsewhere, but additional new findings in these landmasses, along with the discovery of Cretaceous birds in Antarctica and Africa, and the recent interest in the pre-Cretaceous bird-like footprints from the latter continent, call for an update of the Gondwanan record. In this paper the Gondwanan record (Fig. 1, Table 1) is reviewed,

including data on paleoenvironment and associated biota, and its contribution to the understanding of the early history of birds is emphasised.

MATERIALS AND METHODS

The taxonomical nomenclature employed here follows the traditional use of the taxon-name Aves. Hence, the term Aves names a clade, defined as the common ancestor of *Archaeopteryx lithographica* and Neornithes (modern birds) and all its descendants (Fig. 2). Gauthier (1986) and others (Perle et al., 1993, 1994; Norell et al., 1993) proposed restricting the taxon-name Aves to the crown-group of Theropoda, that is the common ancestor of all extant forms plus all its descendants. These authors (including myself in some cases) have used the term Avialae to name the clade traditionally regarded as Aves, while the latter term was used to replace the taxon-name Neornithes of the classical ornithological taxonomy. Perhaps the most attractive advantage of Gauthier's (1986) proposal is the idea of

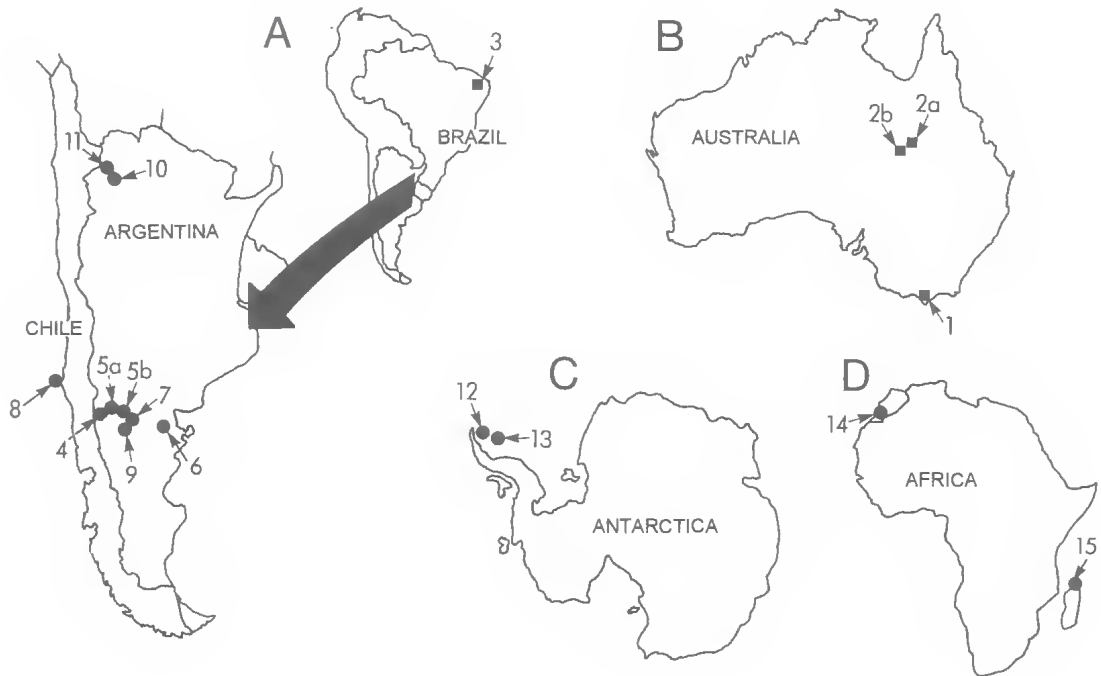


FIG. 1. Maps of A, South America and Argentina-Chile; B, Australia; C, Antarctica; and D, Africa, showing the occurrences of Mesozoic birds. ■ = Early Cretaceous occurrences. ● = Late Cretaceous occurrences. Numbers pointing each locality correspond to those used in Table 1. 1, Koonwarra, Victoria; 2a, 'Warra', Queensland; 2b, 'Canary', Queensland; 3, Santana do Cariri, Ceará; 4, area of Plaza Huincul, Neuquén; 5a, city of Neuquén, Neuquén; 5b, Puesto Tripailao, Río Negro; 6, Estancia Los Alamitos, Río Negro; 7, Salitral Moreno, Río Negro; 8, Bahía San Vicente, Concepción; 9, area of Ingeniero Jacobacci and 'Monton-110', Río Negro; 10, El Brete, Salta; 11, Quebrada del Tapon, Salta; 12, Cape Lamb, Vega Island; 13, Marambio (Seymour) Island; 14, area of Agadir (Morocco); 15, Berivotra, Mahajanga (Madagascar).

having a widely used term, such as Aves, associated with a clade that can be diagnosed by numerous synapomorphies (many soft-tissue characters in addition to the osteological ones). It should be noted, however, that many of these characters (e.g., soft-tissue characters) have an ambiguous optimization when fossils are included in the analysis. The greatest argument against this proposal appears to be simply the universal way in which the name Aves has been associated to the clade composed of all birds (note that a phylogenetic definition is given above) during the last 130 years. Names are terms applied to a definition and ideally they should be conventional. For this reason I would keep using the term Aves in the way it is defined above. The casual terms 'birds' and 'modern birds' refer to Aves and Neornithes, respectively. The collective expression 'non-avian theropods' is used without any systematic meaning.

Several of the occurrences here regarded as Mesozoic birds are represented by footprints. It is well known that the identification of a footprint with a particular trackmaker always involves some degree of uncertainty. Several factors such as the stance, march, speed and the composition of the substrate may affect the morphology of the footprint and consequently its taxonomic interpretation (Padian & Olsen, 1984; Unwin, 1989). In this paper, the recognition of a footprint as avian is based primarily on the criteria summarised by Lockley et al. (1992). Most significant criteria used by Lockley et al (1992) are: 1) small size; 2) slender digit impressions with undifferentiated pad impressions; 3) wide divarication angle between digits II and IV; 4) plantarily directed hallux; 5) slender claws; and 6) distal curvature of lateral claws away from the axis of the pes.

The treatment of the avian occurrences of a particular continent are organised in the follow-

TABLE 1. Avian occurrences in the Mesozoic of Gondwana. Alb=Albian, Apt=Aptian, Bar=Barremian, Cam=Cambrian, Con=Coniacian, Mae=Maastrichtian, Tur=Turonian, San=Santonian.

TAXON	DISTRIBUTION	HORIZON/AGE	EVIDENCE	REFERENCE	
AUSTRALASIA					
1	Aves indet.	Koonwarra, Victoria	Strzelecki Group, Bar-Apt	feather	Talent et al., 1966; Rogers, 1987
2a,b	Enantiornithes: <i>Nanantilus eas</i>	Warra Station (2a), Canary (2b), Queensland	Toolebuc Fm., Alb	bone	Molnar 1986; Molnar pers. comm.
SOUTH AMERICA					
3	Aves indet.	Santana de Cariri, Ceará, Brazil	Santana Fm., Apt- Alb	feather	Martins-Neto & Kellner, 1988; Kellner, 1990
4	Alvarezsauridae: <i>Pataganykus puertai</i>	Area of Plaza Huincul, Neuquén, Argentina	Río Neuquén Fm., Tur-Con	bone	Novas & Coria, 1990; Novas, this volume
5a	Alvarezsauridae: <i>Alvarezsaurus calvoi</i>	City of Neuquén, Neuquén, Argentina	Río Colorado Fm., Con-San	bone	Bonaparte, 1991; Novas, this volume
5a	<i>Patagapteryx deferrariisi</i>	City of Neuquén, Neuquén, Argentina	Río Colorado Fm., Con-San	bone	Alvarenga & Bonaparte, 1992; Chiappe, 1992a
5a,b	Enantiornithes: <i>Neuquenornis valans</i>	City of Neuquén, Neuquén; Puesto Tripailao, Río Negro, Argentina	Río Colorado Fm., Con-San	bone	Chiappe, 1992a; Chiappe & Calvo, 1994
6	Ornithothoraces indet.	Estancia Los Alamos, Río Negro, Argentina	Los Alamos Fm. Cam-Mae	bone	Chiappe, 1992a
7	Ornithurae indet.	Salitral Moreno, Río Negro, Argentina	Allen Fm., Cam-Mae	bone	Powell, 1987; Chiappe, 1992a
8	Ornithurae: Gaviidae: <i>Neogaornis wetzeli</i>	Bahía San Vicente Concepción, Chile	Quiriquina Fm., Cam-Mae	bone	Lambrecht, 1929; Olson, 1992
9	Aves indet.: "Pataganichormis <i>venetiarius</i> "	Area of Ingeniero Jacobacci, "Monton-110", Río Negro, Argentina	Unknown Fm., Mae	ichnite	Casamiquela, 1987; Leonardi, 1987; Chiappe, 1991
10	Enantiornithes indet.	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1991
10	Enantiornithes: <i>Enantiornis leali</i>	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1991
10	Enantiornithes: <i>Soraavisaurus australis</i>	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1993
10	Enantiornithes: <i>Lectavis bretincola</i>	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1993
10	Enantiornithes: <i>Yungavalucris brevipedalis</i>	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1993
11	Aves indet.: <i>Yacoraitichnus avis</i>	Quebrada del Tapón, Salta, Argentina	Yacorait Fm., Mae	ichnite	Alonso & Marquillas, 1986; Chiappe, 1991
ANTARCTICA					
12	Ornithurae: Presbyornithidae indet.	Cape Lamb, Vega Island	López de Bertodano Fm., Cam-Mae	bone	Noriega & Tambussi, 1995
13	Ornithurae: Gaviidae indet.	Marambio (Seymour) Island	López de Bertodano Fm., Cam-Mae	bone	Chatterjee, 1989; Olson, 1992
AFRICA					
14	Aves indet.	Area of Agadir, Morocco	Unknown Fm., Mae	ichnite	Ambroggi & Lapparent, 1954; Lockley et al., 1992
15	Aves indet.	Berivotra, Mahajanga, Madagascar	Maevarano Fm., Cam	bone	Krause, pers. comm.

ing hierarchical arrangement: Aves, Metornithes, Ornithothoraces, Ornithurae, Neornithes. Indeterminate occurrences within a particular clade are listed first.

When anatomical nomenclature is applied, this follows Baumel & Witmer (1993), using the English equivalents of the Latin terminology.

* Taxa recorded in Gondwana

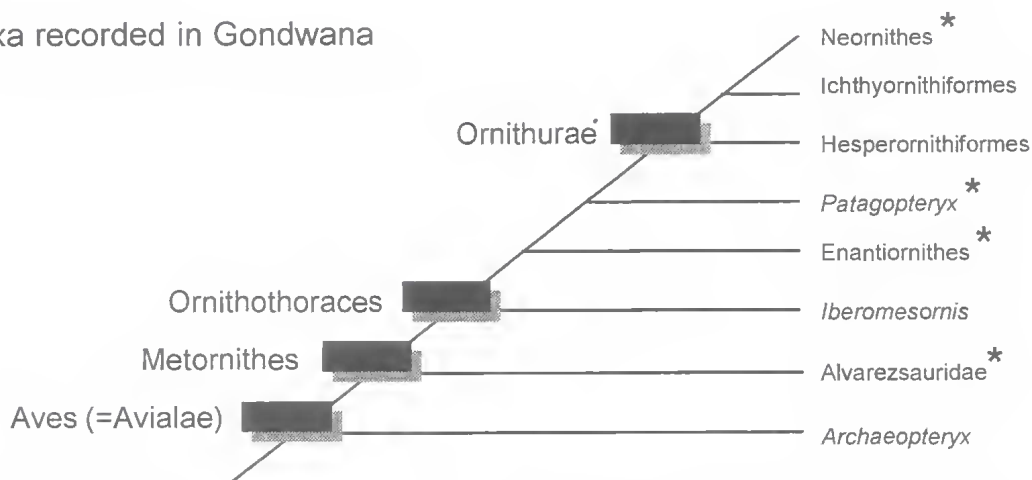


FIG. 2. Cladogram illustrating the relationships between Alvarezsauridae, Enantiornithes, *Patagopteryx deferrariisi* and Neornithes (see Chiappe et al., this volume).

Institutional abbreviations. DNPM, Departamento Nacional da Produção Mineral (Rio de Janeiro, Brazil); GP, Instituto de Geociências, Universidade de São Paulo (São Paulo, Brazil); GPMK, Geologisch-Paläontologisches Institut und Museum, Kiel; LEIUG, Department of Geology, Leicester University (Leicester, United Kingdom); MACN, Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina); MUCPv, Museo de Ciencias Naturales, Universidad Nacional del Comahue (Neuquén, Argentina); NMV, National Museum of Victoria (Melbourne, Australia); PVL, Fundación-Instituto Miguel Lillo, Universidad Nacional de Tucumán (San Miguel de Tucumán, Argentina); PVPH, Museo Carmen Funes (Plaza Huincul, Argentina); QM, Queensland Museum (South Brisbane, Australia); SAMK, South African Museum (Cape Town, South Africa); SMNK, Staatliches Museum für Naturkunde Karlsruhe (Karlsruhe, Germany).

CONTROVERSIAL OCCURRENCES

Ellenberger (1972) described a series of bird-like footprints from the Lower Stormberg beds (Late Triassic) of South Africa, recognising several tridactyl and tetradactyl small ichnospecies (*Trisauropodiscus galliforma*, *T. phasianiforma*, *T. levis*, *T. aviforma*) and other medium size tetradactyls (*T. popompoi*, *T. superaviforma*). Later, Ellenberger (1974) reported several other footprints from the upper Stormberg beds (Early Jurassic) recognising the ichnogrups carnivians (*Masitisauropus*

palmipes, *M. angustus*, *M. exiguus*, *Masitisauropus minimus*, *M. minutus*, *M. perdiciforma*) and lacunavians (*Masitisauropodiscus turdus*, *M. fringilla*). Interestingly, among the carnivians (*M. palmipes*), he claimed the presence of feather-like traces associated to impressions of the thoracic limb. Unfortunately, Ellenberger's descriptions appear to have been made directly in the field, and no holotype or referred specimen has ever been collected and deposited in an institution (Lockley, pers. comm.). This situation limits any comparison to the poorly figured illustrations of his papers (Ellenberger, 1972, 1974). In the case of the feather-like structures (*M. palmipes*), as pointed out by Molnar (1985), there is no compelling evidence to regard these traces as feathers and the footprints themselves are probably not of an avian theropod. The different footprints of *Trisauropodiscus*, however, have the small size and large divarication angle between digits II and IV characteristic of avian trackmakers (Lockley et al., 1992). Lockley et al. (1992) remarked upon the similarity of *Trisauropodiscus* with footprints reported by Ishigaki (1985, 1986) from the Early Jurassic of the Atlas Mountains in Morocco, pointing out that they would have been considered as being made by an avian trackmaker if they were of late Mesozoic age. However, the existence of pre-Late Jurassic birds has yet to be documented. The recent allocation of *Protoavis texensis* (Chatterjee, 1987, 1991) within Aves is not supported by the available evidence. Several authors have expressed their scepticism of Chatterjee's claims (see Ostrom, 1987, 1991; Anderson, 1991;

Monastersky, 1991), and after examination of the material, I also disagree with his hypothesis (Chiappe, 1995a). Therefore, given the fact that indisputable pre-Late Jurassic birds are yet to be documented in addition to the problems associated with the nature of footprints (see Materials and Methods), I prefer to leave these tracks out of the discussion of true birds.

Dettmann et al. (1992: note added in proof) mentioned the discovery of new avian fossils from the Early Cretaceous (Albian) Griman Creek Formation at Lightning Ridge (north-central New South Wales, Australia). Thanks to R.E. Molnar, I had the opportunity to examine casts of this material which comprise the distal ends of two small bones, possibly tibiotarsi. The specimens are fragmentary and I am not completely confident of their identification as tibiotarsi. However, if they are tibiotarsi, then the proximal tarsals are completely fused to the tibia and the fibula does not reach the tarsus. These two characteristics are unique of avians among dinosaurs (Gauthier, 1986; Cracraft, 1986; Chiappe & Calvo, 1994; Chiappe, 1995b, 1996), and support Dettmann's et al. (1992) allocation. In light of the fragmentary condition of these specimens, however, I would wait for further evidence before regarding them as truly avian.

The occurrence of a putative bird bone was mentioned by Smith (1988) in his analysis of the paleoenvironment of a Late Cretaceous crater-lake in Stompoo, central South Africa. Unfortunately, this specimen (SAMK-6486) is a fragmentary left femur and is missing the distal end and most of the proximal one. Although hollow, small and bird-like in aspect, SAMK-6486 does not show any character that can be regarded as avian.

Mussi & Alonso (1989) reported an isolated bird footprint from the Late Cretaceous (Maastrichtian) deposits of the Yacoraite Formation at Dique Cabra Corral (Province of Salta, Argentina). In my opinion this 'footprint' is actually a peculiar disposition of small concretions embedded in the limestone slab and not a track made by a living organism.

Finally, in 1991 I commented on the occurrence of a fragmentary carpometacarpus from the Late Cretaceous (Maastrichtian) Bauru Formation of southern Brazil (Chiappe, 1991). Alvarenga (pers. comm.), however, has recently identified this bone as the extant Yellow-billed cuckoo (*Coccyzus americanus*), being the result of contamination of the Cretaceous material.

THE AVIAN RECORD

AUSTRALASIA

AVES Linnaeus, 1758

MATERIAL EXAMINED. At least five feathers (Fig. 3A), including covert and down ones (Talent et al., 1966; Waldman, 1970; Rogers, 1987; Vickers-Rich, 1991). Waldman (1970) and Rogers (1987) published on NMV P.26059A and P.26059B, slab and counter-slab, respectively.

LOCALITY AND HORIZON. Koonwarra, southeast Victoria, Australia. Strzelcecki Group, Early Cretaceous (Aptian; Vickers-Rich, 1991; Dettmann et al., 1992).

REMARKS. These feathers (Fig. 3A) represent the oldest evidence of birds from this continent. Rogers (1987) studied NMV P.26059A and P.26059B in detail. This feather, regarded as either a primary covert or an alular, was found to be different from any modern feather (Rogers, 1987). This is interesting considering that the only avian material from the Cretaceous of Australia that allows a more precise taxonomic identification belongs to the Enantiornithes (see below), a group not closely related to modern birds (Fig. 2).

The lacustrine mudstones of Koonwarra have provided one of the best Mesozoic continental biota from Australia, including a diversified flora (e.g., bryophytes, ferns, conifers and angiosperms; see Douglas & Williams, 1982), and a large variety of insects, crustaceans, spiders, earthworms, bryozoans, bivalves and fishes (Dettmann et al., 1992). This biotic association becomes of particular interest considering that southeastern Victoria was situated in polar latitudes (~75°-85°S) during the early Cretaceous (Vickers-Rich & Rich, 1989). Douglas & Williams (1982) interpreted the paleoenvironment at Koonwarra as forested (primarily evergreen forests) in a warm to cool-temperate climate with moderate seasonality. However, Vickers-Rich & Rich (1989) emphasised the possibility of annual near-freezing conditions and a prolonged polar night.

METORNITHES Perle et al., 1993
ORNITHOTHORACES Chiappe, 1995
ENANTIORNITHES Walker, 1981

Nanantius eos Molnar, 1986

MATERIAL EXAMINED. HOLOTYPE: QMF12992 (Fig. 3C), complete left tibiotarsus (Molnar, 1986). REFERRED SPECIMENS: QMF31813, proximal end of a tibiotarsus (Molnar & Kurochkin, in press).

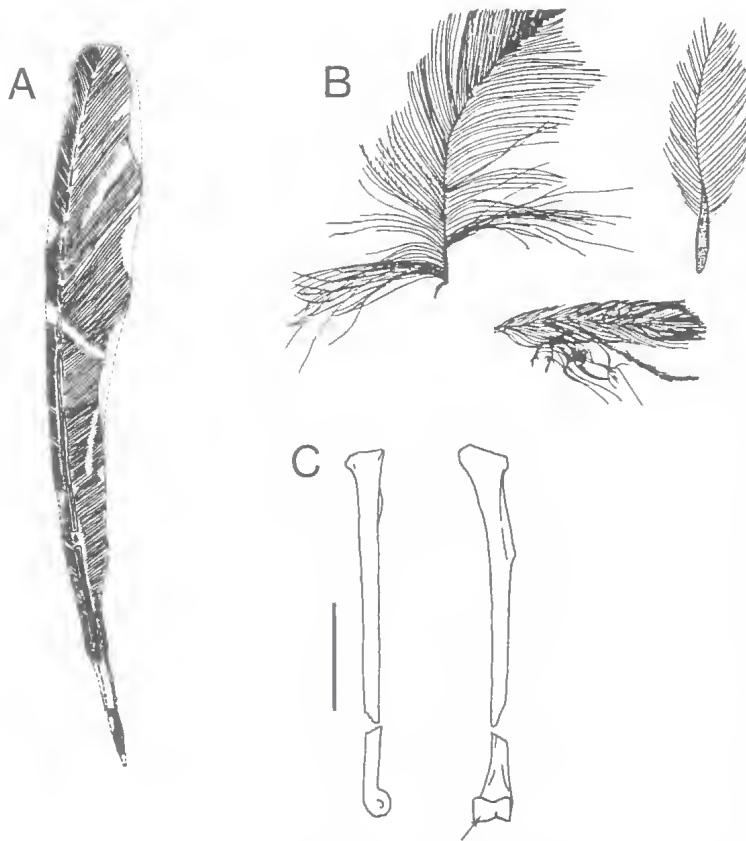


FIG. 3. Early Cretaceous birds from South America and Australasia. A, isolated feather (GP/2T-136) from the Late Aptian Crato Member of the Santana Formation near Santana do Cariri, northeastern Brazil (after Martins Neto & Kellner, 1987). B, Aptian feathers from the Strzelecki Group at Koonwarra, southeastern Victoria, Australia (after Vickers-Rich, 1976). C, medial (left) and cranial (right) views of the tibiotarsus (QMF12992) of *Nanantius eos* from the Albian Toolebuc Formation at Warra Station, western Queensland, Australia (after Molnar, 1986). Arrow points to the broad medial condyle characteristic of enantiornithine birds. In C scale = 1 cm.

QMF12991, an anterior dorsal vertebra that may also be *Nanantius eos* (Molnar & Kurochkin, in press).

LOCALITY AND HORIZON. QMF12992 and QMF12991 were found at Warra Station, east side of Hamilton River near Boulia, west Queensland, Australia. QMF31813 is from Canary Station in west Queensland, Australia. Toolebuc Formation, Early Cretaceous (Albian; Molnar, 1986; Dettmann et al., 1992).

REMARKS. Molnar (1986) correctly placed *Nanantius eos* into the Enantiornithes. The tibiotarsus of *N. eos* shows a round proximal articular surface, a smooth craniolateral cnemial crest, and a wide and bulbous medial condyle (Fig. 3C), which are enantiornithine synapomor-

phies (Chiappe, 1992b, 1993). *N. eos* is a small enantiornithine, approximately the size of the American robin (*Turdus migratorius*) (Molnar, 1986). Nevertheless, the complete fusion of the proximal tarsals to the tibia in the holotype of *N. eos* suggests that this represents an adult individual. The size of *N. eos* is significantly smaller than any of the South American enantiornithines, and comparable to the size of the enantiornithines *Alexomis antecedens* (Brodkorb, 1976) and *Concomis lacustris* (Sanz et al., 1995) from the Cretaceous of Mexico and Spain, respectively.

Molnar & Kurochkin (in press) have identified QMF-31813 as *Nanantius* sp. remarking on a few subtle differences with respect to *Nanantius eos*. In my opinion, this specimen should be placed within *N. eos*. QMF12991, found at less than 5 cm from the holotype of *N. eos*, may also belong to this species (Molnar & Kurochkin, in press), but these authors have pointed out that it belongs to an individual larger than the holotype of this species.

The Toolebuc Formation is composed of offshore marine limestones deposited during the middle-late Albian (Molnar & Thulborn, 1980; Dettmann et

al., 1992). The holotype specimen was associated with fish remains, turtles, ichthyosaurs and pterosaurs (Molnar, 1986). The common occurrence of fossil logs within these deposits might indicate that the shoreline was forested near the type locality of *Nanantius eos* (Dettmann et al., 1992). *N. eos* is the only occurrence of a Gondwanan enantiornithine in marine deposits.

SOUTH AMERICA

AVES Linnaeus, 1758

MATERIAL EXAMINED. SEVERAL ISOLATED FEATHERS: GP/2T-136 (Fig. 3B), a flight feather (Martins-Neto & Kellner, 1988); DNPM MCT 1493-R,

a down feather (Kellner et al. 1994); LEIUG 114369, a semiplume (Martill & Filgueira, 1994); LEIUG 115562, SMNK 1247 PAL (counterpart), a contour, body feather (Martill & Frey, 1995).

LOCALITY AND HORIZON. All feathers are from the Ararape Basin in the State of Ceará, Brazil. GP/2T-136 and DNPM MCT 1493-R come from an indeterminate area around Nova Olinda (Kellner, pers. comm.); LEIUG 115562, SMNK 1247 PAL and LEIUG 114369 are from the Mina de Antone Phillippe, near Tatajuba. Santana Formation, Crato Member, Early Cretaceous (Late Aptian; Pons et al., 1990).

REMARKS. GP/2T-136 is a fairly small feather (approximately 64mm long), which might have belonged to a bird of the size of the neotropical brush finches (*Atlapetes*) (Kellner et al., 1991). It has a strong rachis and a very narrow outer vane (Kellner et al., 1991). The fact that this feather has asymmetric vanes (Fig. 3B) suggests it belonged to a flying bird (Feduccia & Tordoff, 1979), although no taxonomic assignment is possible with only this evidence. In LEIUG 115562 (and its counterpart, SMNK 1247 PAL), a small body feather, the color patterning is preserved. This consists of a series of transverse dark and light bands (Martill & Frey, 1995). Barbules have been preserved in both DNPM MCT 1493-R and LEIUG 114369 (Kellner et al., 1994; Martill & Filgueira, 1994). The presence of semiplumes, flight, body and down feathers in the Crato Member highlights the differentiation of feather types as early as the Early Cretaceous.

The paleoenvironment of the Crato Member has been generally regarded as a calm, fresh water lake existing under arid climatic conditions (Maisey, 1991), although restricted connections to marine waters may have existed (Martill & Filgueira, 1994; Martill & Frey, 1995). Sediments consist of laminated limestones with intervening beds of sands and shales (Maisey, 1991; Martill & Filgueira, 1994). The feathers were found in the laminated limestones, regarded as the marginal lake facies (Kellner et al., 1991; Martill & Filgueira, 1995). The fossil assemblage recorded from the Crato Member includes an abundant variety of insects (Grimaldi, 1990), along with scorpions, spiders, fishes, frogs and several floral elements (Maisey, 1991).

***Yacoraitichnus avis* Alonso & Marquillas,
1986**

MATERIAL EXAMINED. Slab (without number when published) with several footprints (Fig. 4A) (Alonso & Marquillas, 1986; Alonso, 1989).

LOCALITY AND HORIZON. Quebrada del Tapón, Valle del Tonco, Department of San Carlos, Province of Salta, Argentina. Yacoraite Formation, Late Cretaceous (Maastrichtian; Alonso & Marquillas, 1986).

REMARKS. *Yacoraitichnus avis* consists of medium size footprints (approximately 80mm long), lacking the hallux impression (Alonso & Marquillas, 1986) (Fig. 4A). This ichno-species is one of the few avian tracks that shows digital pad impressions (Lockley et al., 1992). Alonso & Marquillas (1986) suggested that *Y. avis* could either belong to a galliform-like neognathine or to an enantiornithine bird, although they finally regarded it as indeterminate among avians. The hypothesis of a galliform affinity becomes unlikely considering that the earliest known galliform comes from the Early Eocene of North America. Likewise, despite the fact that diverse ensemble of enantiornithine birds is known from the Lecho Formation (see below) — a unit considered to be part of the same depositional event of the Yacoraite Formation (Gomcz Omil et al., 1989) — no ichnites have been ever found associated with these and other enantiornithine remains making the latter hypothesis untestable (Chiappe, 1991).

The footprints of *Yacoraitichnus avis* occur in a narrow band of green claystone one meter above deposits with a variety of non-avian dinosaur footprints (Alonso & Marquillas, 1986; Alonso, 1989). Remains of fishes and crocodiles are also known to occur in the Yacoraite Formation at Quebrada del Tapón (Alonso & Marquillas, 1986). The footprints at Quebrada del Tapón occur in coastal plain beds deposited along the western margin of an extensive body of water (Alonso, 1989). This coastal plain was periodically submerged because of changes in the level of the water. Alonso (1989) concluded that the footprints of *Y. avis* were produced on an exposed layer of mud, left after a period of inundation.

**'Patagonichnornis venetiorum' Casamiquela,
1987**

MATERIAL EXAMINED. Footprints (no repository has been published; see Casamiquela, 1987).

LOCALITY AND HORIZON. Area of Ingeniero Jacobacci and 'Monton-110', Province of Rio Negro, Argentina. The footprints from around Ingeniero Jacobacci are referred to the Late Cretaceous without any further stratigraphical information (see Casami-



FIG. 4. Late Cretaceous footprints from South America and Africa. A, *Yacoraitichnus avis* from the Maastrichtian Yacoraite Formation at Quebrada del Tapón, Province of Salta, Argentina (after Alonso & Marquillas, 1986). B, C, D, bird tracks from Maastrichtian deposits near Agadir, southern Morocco (after Ambroggi & Lapparent, 1954).

quela, 1987); the ones from 'Monton-110' are listed as Late Maastrichtian (see Leonardi, 1987: Plate XVIII).

REMARKS. Casamiquela (1987) reported the discovery of bird footprints associated with tracks of hadrosaurs and, although they were neither described nor illustrated, he named them '*Patagonichnormis venetiorum*'. On the other hand, a cast with several bird tracks from the Late Maastrichtian of the Argentine Río Negro Province ('Monton-110') was illustrated by Leonardi (1987), although no further geographical reference was given. These latter tracks have long, slender digits and large divaricate angles between digits II and IV (Leonardi, 1987). Although not verified, it is likely that Leonardi (1987) was illustrating what Casamiquela (1987) named '*P. venetiorum*'.

Casamiquela (1987) allocated '*Patagonichnormis venetiorum*' in the extinct Cimolopterygidae within the Charadriiformes, the group that includes most extant shorebirds. As I have previously pointed out (Chiappe, 1991), there is no evidence to support such taxonomic allocation. The Cimolopterygidae are only known from elements of the forelimb and thoracic girdle (Brodkorb, 1963a; Olson & Parris, 1987; Tokaryk & James, 1989), and they are not the only Cretaceous charadriiforms (Olson, 1985; Olson & Parris, 1987). Furthermore, there are other shorebirds in the Cretaceous, such as *Gansus yumenensis* from the Early Cretaceous of China (Hou & Liu, 1984) and a new Presbyornithidae from the Late Cretaceous of Antarctica (Noriega & Tambussi, 1995; see below). Moreover, the morphology of the hind limb of the enantiornithine *Lectavis bretincola* from the Late Cretaceous Argentine Province of Salta (Chiappe, 1993; see below) suggest wading habits (Walker, 1981), making it equally likely that the footprints from Ingeniero Jacobacci belonged to an enantiornithine bird. Due to the lack of information, I

prefer to consider the identity of these footprints as indeterminate among avians.

METORNITHES Perle et al., 1993
ALVAREZSAURIDAE Bonaparte, 1991

Patagonykus puertai Novas, this volume

MATERIAL EXAMINED. HOLOTYPE: PVPH-37, isolated dorsal, synsacral and caudal vertebrae, along with portions of thoracic limb and coracoids, and pelvic girdle and limb (see Novas, this volume; in press).

LOCALITY AND HORIZON. Sierra del Portezuelo, Province of Neuquén, Argentina. Río Neuquén Formation, Late Cretaceous (Turonian-Coniacian; Legarreta & Gulisano, 1989).

REMARKS. *Patagonykus puertai* is unquestionably a new taxon, although the actual association of the different elements of PVPH-37 into a single individual or even a single species may be questionable (Chiappe et al., this volume). As emphasised by Novas (this volume; in press; see also Chiappe et al., this volume), several characters in the synsacrum, pelvic girdle and thoracic limb indicate a close relationship between *P. puertai*, the Patagonian *Alvarezsaurus calvoi* (Bonaparte, 1991; see below) and *Mononykus olecranus* from the Late Cretaceous of central Asia (Perle et al., 1993, 1994). *P. puertai* had the bizarre morphology of the thoracic limb of *M. olecranus* (Perle et al., 1993, 1994), but this bird was significantly larger than its closest relatives, being about the size of the non-avian theropod *Deinonychus antirrhopus* (Novas & Coria, 1990).

The Río Neuquén Formation is composed of fluvial deposits (Cazau & Uliana, 1973). In addition to *Patagonykus puertai*, this formation has provided remains of fishes, amphibians, turtles and titanosaurid dinosaurs (Novas & Coria, 1990; Bonaparte, 1992; Novas, pers. comm.).

Alvarezsaurus calvoi Bonaparte, 1991

MATERIAL EXAMINED. HOLOTYPE: MUCPv-54, articulated specimen including several cervical and dorsal vertebral remains, three synsacral and 13 caudal vertebrae, a scapula and part of a coracoid, portions of both ilia, femora, tibiae and proximal tarsals, and metatarsals and pedal phalanges (Bonaparte, 1991).

LOCALITY AND HORIZON. City of Neuquén, Province of Neuquén, Argentina. Río Colorado Formation, Bajo de la Carpa Member, Late Cretaceous (Coniacian-Santonian; Chiappe & Calvo, 1994).

REMARKS. Novas (this volume) included *Patagonykus puertai* and *Mononykus olecranus* along with *Alvarezsaurus calvoi* in the Alvarezsauridae, a taxon recognised by Bonaparte (1991) to include the latter species. Bonaparte (1991) remarked on the differences of alvarezsaurids to all theropods then known. In fact, this distinction was emphasised by his creation of the Alvarezsauria, a taxon that included both Alvarezsauridae and *A. calvoi*. Alvarezsauria, however, should be disregarded in that it only adds redundancy to the taxonomic system. Chiappe et al. (this volume) have presented evidence for the avian affinity of *A. calvoi*, which along with all alvarezsaurids are the sister-group of all birds other than *Archaeopteryx lithographica*.

The fluvial sandstones of the Bajo de la Carpa Member in the city of Neuquén have provided abundant remains of continental tetrapods such as the flightless bird *Patagopteryx deferrariisi* (Alvarenga & Bonaparte, 1992; see below), the enantiornithine bird *Neuquenomis volans* (Chiappe & Calvo, 1994; see below), notosuchian and baurusuchid crocodiles, dynilid ophidians, small non-avian theropods, and titanosaurid sauropods (Bonaparte, 1991; Chiappe & Calvo, 1994). The beds of the Bajo de la Carpa Member have been regarded as high energy channels, deposited in a paleoenvironment of braided streams (Cazau & Uliana, 1973). In the area of the city of Neuquén, however, the characteristics of the fossil fauna and its preservation (i.e., small, articulated tetrapods, absent in other localities) suggest a lower energy depositional environment than the one envisioned previously (Chiappe & Calvo, 1994).

ORNITHOTHORACES Chiappe, 1995

MATERIAL EXAMINED. MACN-RN-976 (Fig. 5), an isolated cervical vertebra.

LOCALITY AND HORIZON. Estancia Los Alamitos, Cerro Cuadrado, Province of Río Negro, Argentina

(Bonaparte et al., 1984; Bonaparte, 1986. Los Alamitos Formation, Late Cretaceous (Campanian-Maastrichtian; Bonaparte, 1987).

REMARKS. This is the only avian specimen so far recorded from the rich fossil fauna of the Los Alamitos Formation (Bonaparte et al., 1984; Bonaparte, 1987, 1990). The presence of a well-developed ventral process (Figs 5F, G) indicates that MACN-RN-976 was a caudal element within the cervical series. MACN-RN-976 has a fully heterocoelic centrum (Figs 5F, G) and in this respect differs from both *Patagopteryx deferrariisi* and Enantiornithes in which the posterior cervicals have an incipient degree of heterocoely (Chiappe, 1992a, 1996). The presence of heterocoelic cervical vertebrae (including an incipient degree of development) diagnoses the clade formed by the common ancestor of Enantiornithes and modern birds plus all its descendants (unnamed node; see Chiappe, 1992a, 1995b, 1996; Chiappe & Calvo, 1994). The fragmentary nature of MACN-RN-976 makes it difficult to be more specific in its allocation.

The mudstone to sandstone deposits of Los Alamitos Formation at Cerro Cuadrado have yielded abundant remains of invertebrates, fishes, frogs, snakes, turtles, mammals and non-avian dinosaurs (Bonaparte et al., 1984; Bonaparte, 1987, 1990). Paleoenvironmentally, this formation has been interpreted as a shallow, permanent brackish body of water (Andreis, 1987; Bonaparte, 1990).

Patagopteryx deferrariisi
Alvarenga & Bonaparte, 1992

MATERIAL EXAMINED. HOLOTYPE: MACN-N-03, a partially complete specimen including several cervical, thoracic, synsacral and caudal vertebrae, portions of the wing and shoulder, part of the ilium and hind limb elements (Alvarenga & Bonaparte, 1992; Chiappe, 1992). REFERRED SPECIMENS: MACN-N-11 (Fig. 6), an almost complete skeleton; MUCPv-48 (Fig. 6), a complete hind limb associated with several fragmentary bones; MACN-N-10, MACN-N-14 and MUCP-207, fragmentary specimens (Chiappe, 1992a).

LOCALITY AND HORIZON. City of Neuquén, Province of Neuquén, Argentina. Río Colorado Formation, Bajo de la Carpa Member, Late Cretaceous (Coniacian-Santonian; Chiappe & Calvo, 1994).

REMARKS. *Patagopteryx deferrariisi* is a hen-sized, flightless bird known from the same deposits as *Alvarezsaurus calvoi* (see above). Alvarenga & Bonaparte (1992) and Alvarenga

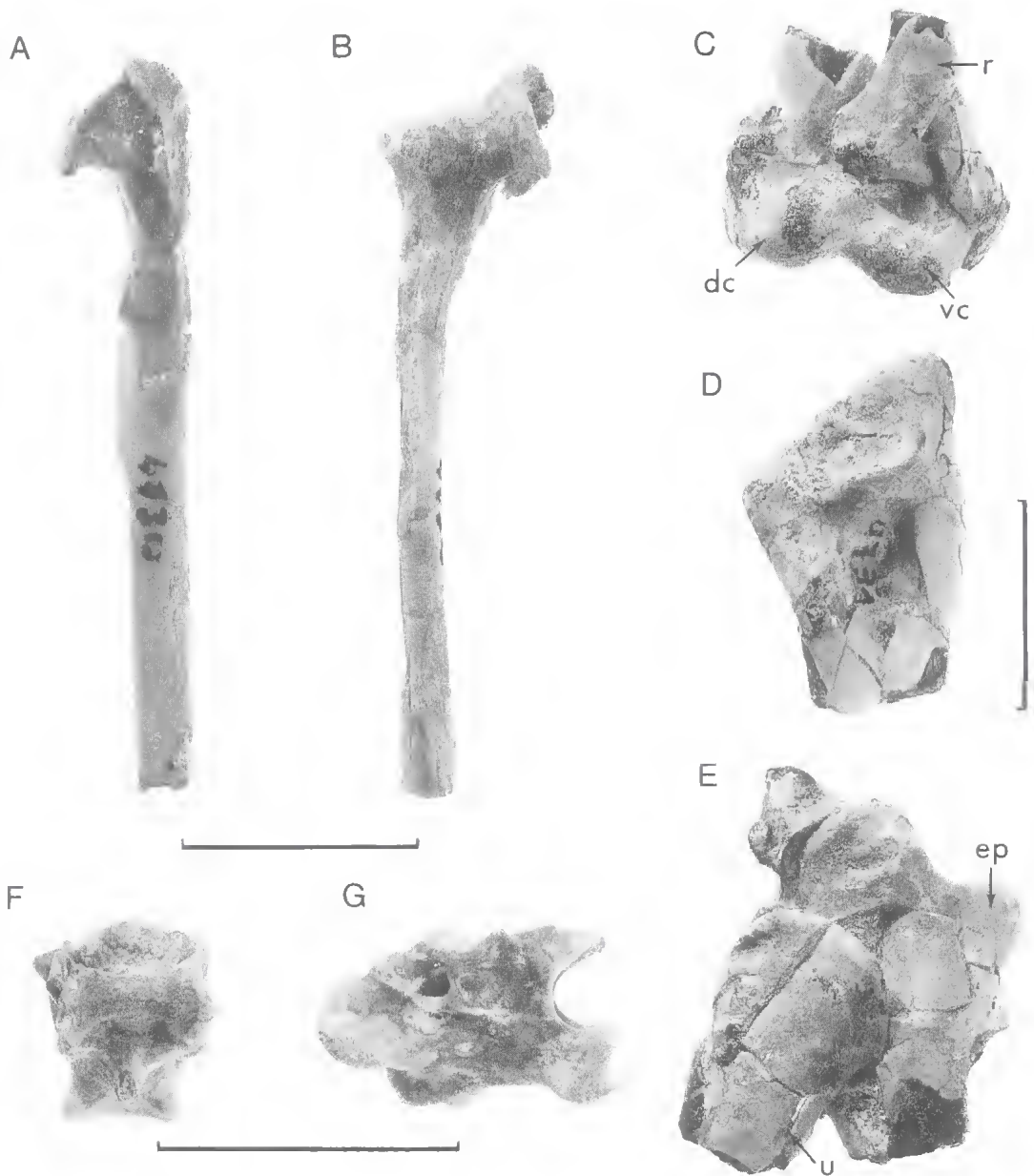


FIG. 5. Ornithurine specimens from the Maastrichtian Allen Formation at Salitral Moreno (A-E), and the Campanian-Maastrichtian Los Alamos Formation at Estancia Los Alamos, Province of Río Negro, Argentina. A, B, proximal half of left tibiotarsus (PVL-4730) in cranial (A) and lateral (B) views; C, distal end of the right humerus (PVL-4731) in cranial view (the radius is still articulated); D, proximal end of right ulna (PVL-4731) in ventral view; E, distal and proximal ends of right ulna and carpometacarpus (PVL-4731) in caudal and dorsal views, respectively. F, G, heterocoelic vertebra (MACN-RN-976) in cranial (F) and left lateral (G) views. dc, dorsal condyle of humerus; ep, extensor process of carpometacarpus; r, radius; u, ulna; vc, ventral condyle of humerus. Scales = 1cm.

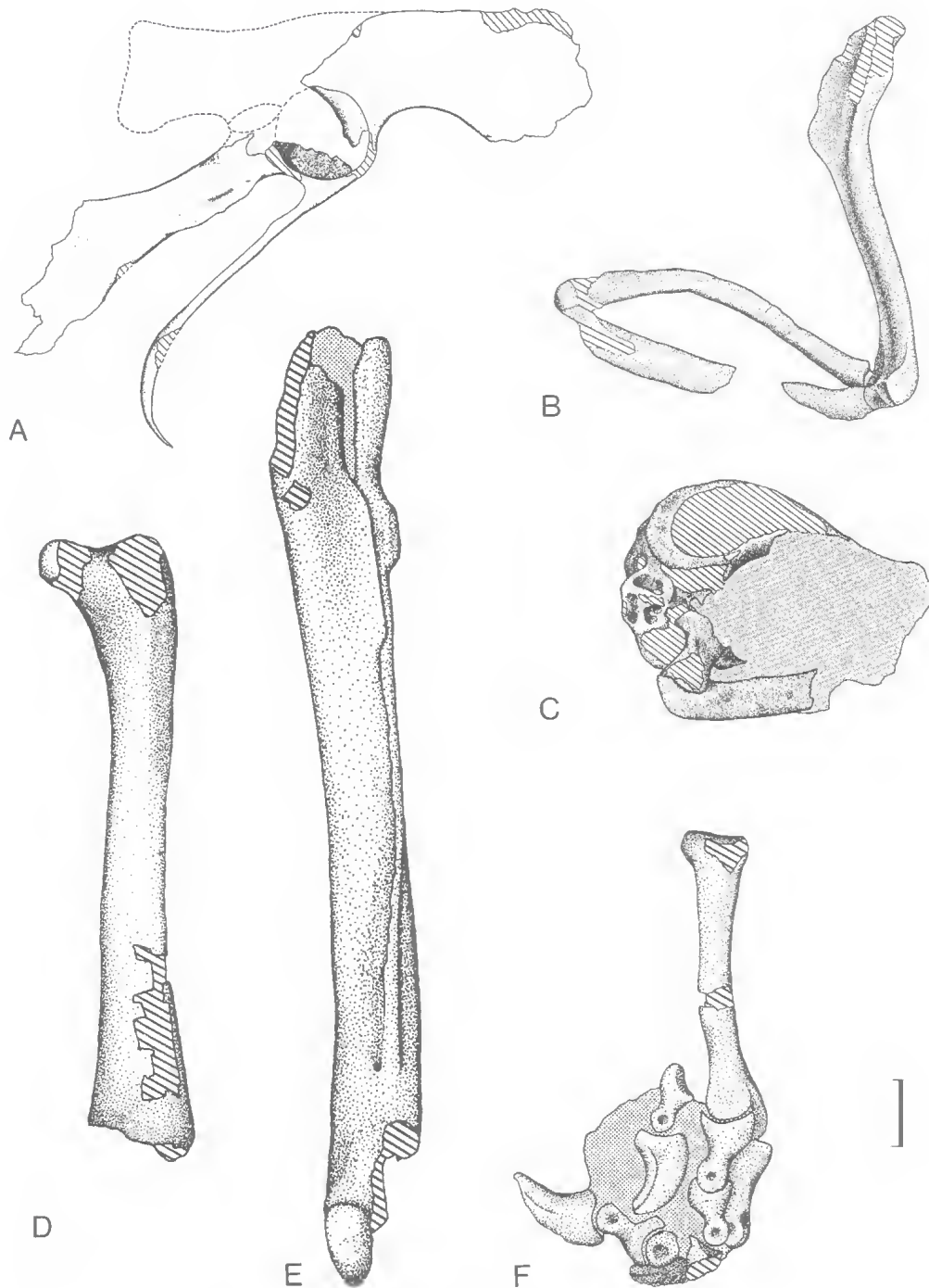


FIG. 6. *Patagopteryx deferrariisi* from the Coniacian-Santonian Río Colorado Formation at the city of Neuquén, Province of Neuquén, Argentina. A, right lateral view of the pelvis (MACN-N-11); B, ventral view of the right humerus, ulna and radius (MACN-N-11); C, right lateral view of the skull (MACN-N-11); D, cranial view of the left femur (MUCPv-48); E, cranial view of the left tibiotarsus and fibula (MUCPv-48); F, medial view of the left tarsometatarsus and phalanges MUCPv-48. Scale = 1cm.

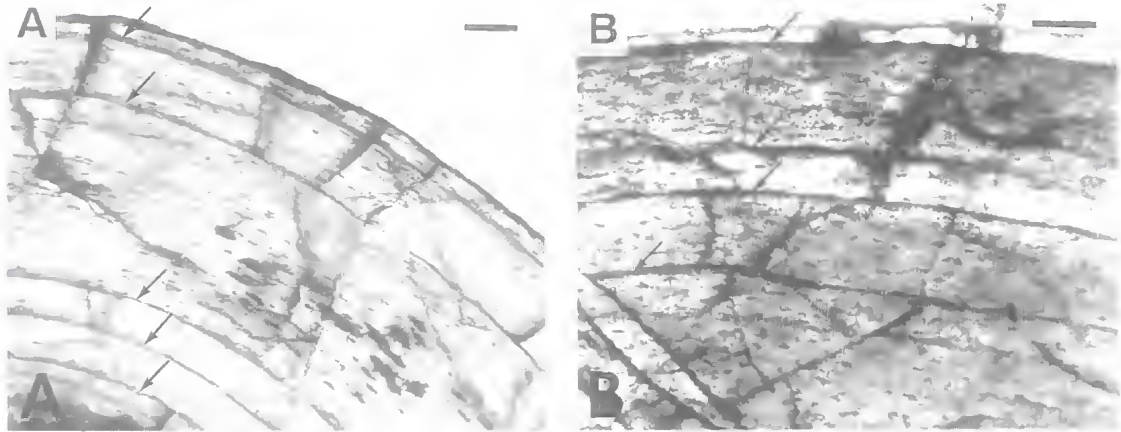


FIG. 7. Transverse sections of the enantiornithine femora of PVL-4273 (A) and MACN-S-01 (B) from the Maastrichtian Lecho Formation at Estancia El Brete, Province of Salta, Argentina. Arrows show different lines of arrested growth (LAGs) in the compacta of these bones. Scales = 100 μ m.

(1993) related this species to the ratites (ostriches and its allies). A more parsimonious interpretation, however, supports the sister-group relationship between *P. deferrariisi* and Ornithurae (Chiappe, 1992a, 1995a, b; Chiappe & Calvo, 1994; Chiappe et al., this volume) (Fig. 2). Furthermore, the hypothesis of ratite affinities has been seriously challenged by recent histological studies documenting the presence of growth rings or lines of arrested growth (LAGs) in the compacta of the femora of both *P. deferrariisi* and the Enantiornithes (Chinsamy et al., 1994, 1995). This pattern of bone microstructure is absent in ornithurine birds, including ratites. The presence of cyclical pauses in bone deposition indicates that *P. deferrariisi*, and the Enantiornithes, had a rate of growth and associated physiology different from that of any modern bird (Chinsamy et al., 1994, 1995). In consequence, compelling osteological and histological evidence supports the hypothesis that *P. deferrariisi* acquired flightlessness independently from ratites and any other known flightless avian group (Chiappe, 1995a, b, 1996).

Curiously, Nesson (1993) recently related the Coniacian *Kuszholia mengi* (Nesson, 1992) from the Bissekty Formation at Dzhyrakuduk (Uzbekistan) to *Patagopteryx deferrariisi*. Nesson (1992) briefly described and illustrated two fragmentary synsacra, which appear to be all the available material, and concluded that *K. mengi* could have been either a bird or a non-avian theropod. Comparisons based on such limited evidence are very hard to make. The synsacrum of *K. mengi*, however, differs from that

of *P. deferrariisi* in the presence of pleurocoels and a concave caudal articular surface.

ENANTIORNITHES Walker, 1981

MATERIAL EXAMINED. Large assortment of postcranial elements and a jaw housed at the Fundación-Instituto Miguel Lillo (Tucumán) and the Museo Argentino de Ciencias Naturales (Buenos Aires) (Walker, 1981; Chiappe, 1993, 1996).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. The Maastrichtian deposits of the Lecho Formation (Gómez Omil et al., 1989) have provided the most diverse and abundant collection of Gondwanan Cretaceous avians (Bonaparte et al., 1977; Bonaparte & Powell, 1980; Walker, 1981; Chiappe, 1991, 1993). Most of these avian remains were preliminarily studied by Walker (1981), who recognised them as part of a basal monophyletic group, the Enantiornithes. The phylogenetic relationships of the Enantiornithines have been a matter of debate (Chiappe, 1995a, b), although most authors regard them as basal birds. Recent cladistic analyses (Chiappe, 1995a, b, 1996; Chiappe & Calvo, 1994; Chiappe et al., this volume) support the hypothesis that the Enantiornithes is the sister-group of the clade formed by *Patagopteryx deferrariisi* and Ornithurae (Fig. 2). The number of species represented in the enantiornithine assemblage of El Brete is not yet known. It is likely,

however, that more than the four named species (see below) are present in this site. The fact that most bones are preserved disarticulated prevents a more precise evaluation of the actual specific diversity.

As mentioned in the discussion of *Patagopteryx deferrariisi*, recent histological studies of enantiornithine femora from this collection have documented the presence of LAGs in the compacta of these bones (Chinsamy et al., 1994, 1995) (Fig. 7). As pointed out by Chinsamy et al. (1994, 1995), cyclical bone deposition in Enantiornithes and other basal birds suggests important physiological differences with respect to their modern relatives.

The avian assemblage from El Brete (including the four species discussed below) is in association with remains of sauropod and non-avian theropod dinosaurs (Bonaparte et al., 1977; Bonaparte & Powell, 1980). The fine-grained sandstone entombing this assemblage has been regarded as deposited in a fluvial-lacustrine coastal plain, with abundant vegetation and ponds (Bonaparte et al., 1977).

Enantiornis leali Walker, 1981

MATERIAL EXAMINED. PVL-4035 (Fig. 8), a specimen including the proximal half of the humerus, the proximal portion of the scapula, and a coracoid (Walker, 1981). **REFERRED SPECIMENS:** PVL-4020, several thoracic limb and girdle elements; PVL-4039, PVL-4055, two isolated scapulae; PVL-4023, PVL-4181, two isolated ulnae.

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. Unfortunately, Walker (1981) never described this species but just listed its name in the figure's caption. Below is a brief description of the holotype specimen. A more detailed description of all the available material would not

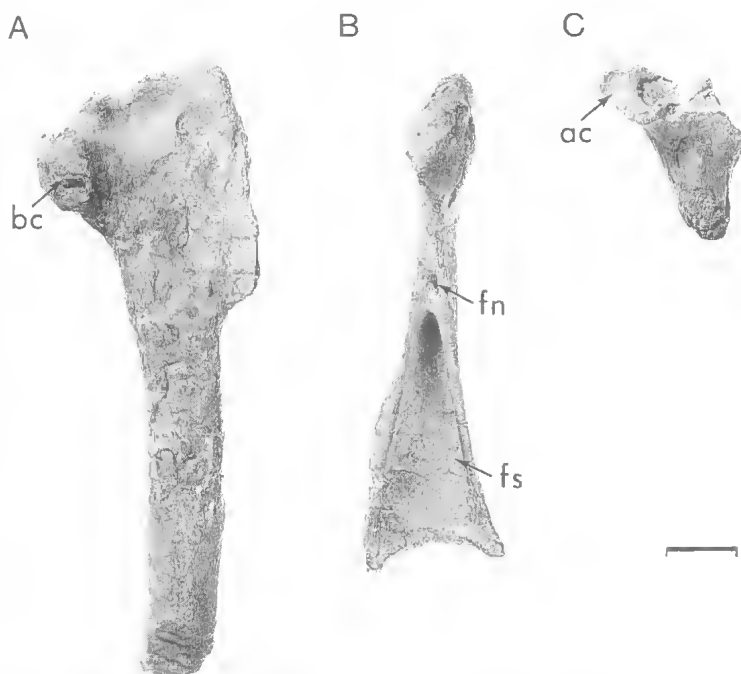


FIG. 8. *Enantiornis leali* (PVL-4035) from the Maastrichtian Lecho Formation at Estancia El Brete, Province of Salta, Argentina. A, proximal half of left humerus in cranial view; B, left coracoid in dorsal view; C, left scapula in medial view. ac=acromion, bc=bicipital crest, fn=foramen for supracoracoid nerve, fs=dorsal fossa of coracoid. Scale = 1cm.

be appropriate for this paper, but it will be provided elsewhere (Chiappe & Walker, in preparation).

The humerus of *Enantiornis leali* is very robust (Fig. 8A). The cranial side of the head is deeply concave. Distal to the head there is a deep, sub-circular fossa. As in other enantiornithines, the bicipital crest is inflated and projected cranioventrally (Fig. 8A). The ventral tubercle is projected caudally and, most peculiarly, it is proximodistally perforated by a foramen. The pneumotricipital foramen is not developed. The coracoid is elongated (Fig. 8B). Its shoulder end is lateromedially compressed and it slopes dorsally. Medially, between the articular facet for the humerus and the acrocoracoid process, there is a subcircular tubercle. As typical of all enantiornithines, the dorsal surface of the coracoid is deeply excavated by a triangular fossa (Fig. 8B). Slightly above the vertex of this fossa is the dorsal opening of the foramen for the supracoracoid nerve. The position of this foramen differs from that in some other enantiornithines, where it opens inside the fossa. The scapula has a well-developed acromion (Fig. 8C). Its most charac-

teristic feature is the presence of a circular pit, medially situated between the acromion and the articular facet for the humerus.

Enantiornis leali was a fairly large bird, ranging between the size of a skua (*Catharacta skua*) and a turkey vulture (*Cathartes aura*). This species is represented by elements of the thoracic limb and girdle only, while all other named enantiornithine species from El Brete are known from elements of the pelvic limb (Chiappe, 1993). Thus, there is the possibility that *E. leali* might be a synonym of one of the three other enantiornithine species from El Brete.

Lectavis bretincola Chiappe, 1993

MATERIAL EXAMINED. HOLOTYPE: PVL-4021-1 (Fig. 9A, B), a tibiotarsus and tarsometatarsus missing the distal portion (Chiappe, 1993).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. The pedal morphology of *Lectavis bretincola* together with the inflation of the medial condyle of the tibiotarsus (Chiappe, 1993; Chiappe & Calvo, 1994) supports the allocation of this taxon in the Enantiornithes. The phylogenetic relationships of *L. bretincola* to other enantiornithines are not clearly understood, although a recent cladistic analysis indicates that this taxon lies outside the Avisauridae a group of small to medium size arboreal enantiornithines (Chiappe, 1993; see below). The very elongate tibiotarsus and tarsometatarsus of *L. bretincola* (Fig. 9A, B) suggest that it had wading habits (Walker, 1981).

Yungavolucris brevipedalis Chiappe, 1993

MATERIAL EXAMINED. HOLOTYPE: PVL-4053 (Fig. 9E, F), a nearly complete tarsometatarsus. REFERRED SPECIMENS: Several tarsometatarsi (PVL-4040, PVL-4052, PVL-4268, PVL-4692) (Chiappe, 1993).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. The presence of a metatarsal IV far smaller than metatarsals II and III, a tubercle on the dorsal face of metatarsal II, and a trochlea of metatarsal II broader than that of metatarsals II

and IV (Fig. 9E, F), identify this taxon as an enantiornithine (Chiappe, 1993). The phylogenetic relationships of *Yungavolucris brevipedalis* to other enantiornithines are not resolved, however. Like *Lectavis bretincola*, a cladistic analysis within the Enantiornithes indicates that it is not an avisaurid enantiornithine (Chiappe, 1993). The remarkable asymmetry of the tarsometatarsus of *Y. brevipedalis* (Fig. 9E, F) suggests that this species was probably aquatic (Walker, 1981).

AVISAUROIDAE Brett-Surman & Paul, 1985

Soroavisaurus australis Chiappe, 1993

MATERIAL EXAMINED. HOLOTYPE: PVL-4690 (Fig. 9C, D), a tarsometatarsus (Chiappe, 1993). REFERRED SPECIMENS: PVL-4048, a tarsometatarsus articulated to several phalanges (Chiappe, 1993).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. *Soroavisaurus australis* can be regarded as an enantiornithine on the basis of the pedal characteristics mentioned for *Yungavolucris brevipedalis*, in addition to derived features shared with *Neuquenornis volans* (e.g., strong plantar projection of the medial rim of the trochlea of metatarsal III, transverse convexity of dorsal surface of the mid-shaft of metatarsal III; see Chiappe, 1993; Chiappe & Calvo, 1994). The avian affinity of *S. australis* was questioned by Brett-Surman & Paul (1985), who regarded it as non-avian dinosaur, together with *Avisaurus archibaldi* from the Late Cretaceous Hell Creek Formation of North America. The avian affinity of the Avisauridae, however, has been definitively established with the discovery of fairly complete specimens showing undisputable enantiornithine features (Chiappe, 1992b, 1993; Huchinson, 1993; Chiappe & Calvo, 1994).

A recent cladistic analysis (Chiappe, 1993; Varricchio & Chiappe, 1995) indicates that *Soroavisaurus australis* is the sister-group of the North American avisaurids (*Avisaurus archibaldi* and *A. gloriae*). This study demonstrates the non-monophyletic status of the El Brete enantiornithine assemblage, which is composed of taxa sharing a most recent common ancestor with North American taxa. The pedal morphology of

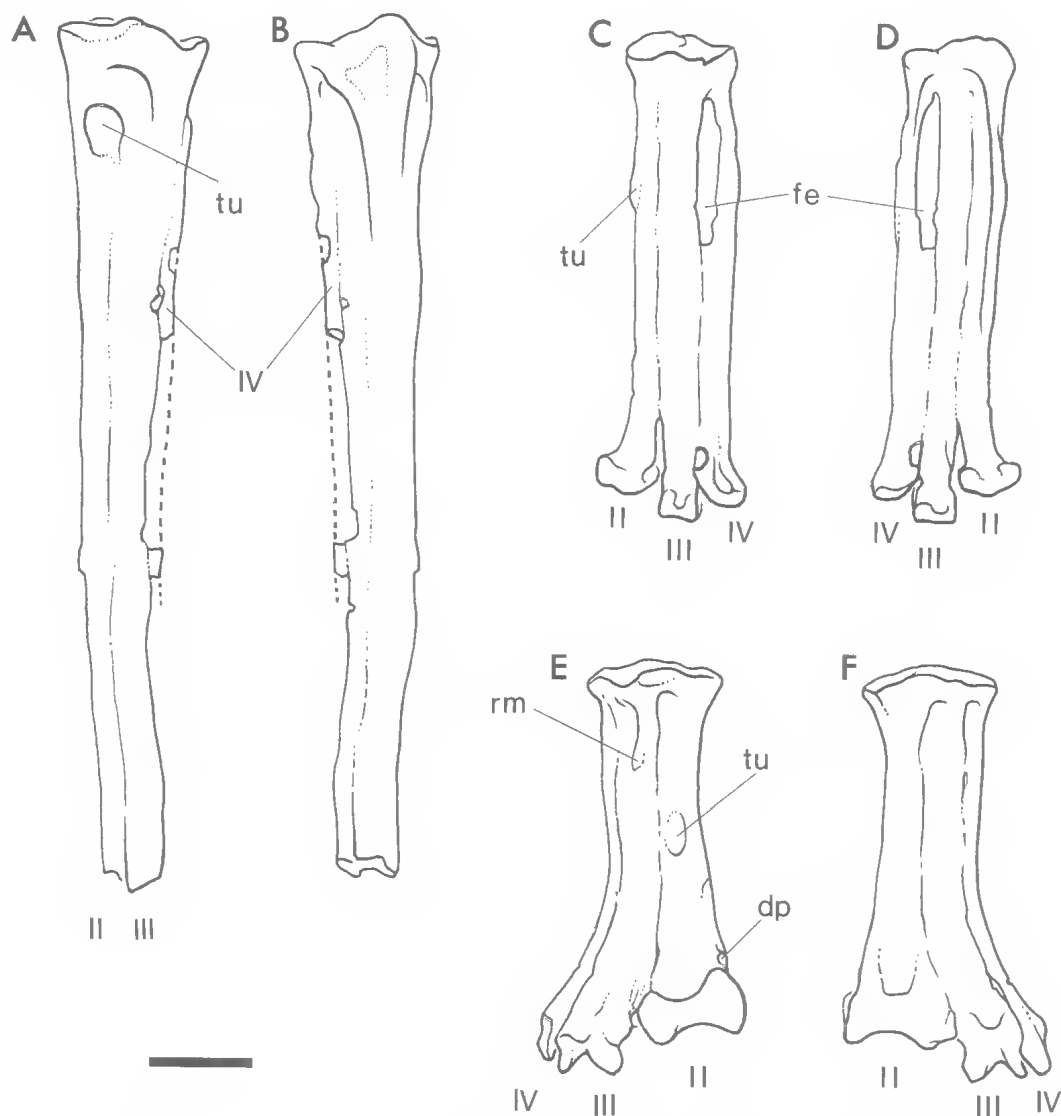


FIG. 9. Enantiornithine tarsometatarsi (dorsal and plantar views) from the Maastrichtian Lecho Formation at Estancia El Brete, Province of Salta, Argentina (after Chiappe, 1993). A, B, *Lectavis bretincola* (PVL-4021-1); C, D, *Soroavisaurus australis* (PVL-4690); E, F, *Yungavolucris brevipedalis* (PVL-4053). dp=dorsomedial projection of the distal end of metatarsal II, fe=fenestra between metatarsals III and IV, rm=elongate proximal ridge for muscle attachment, tu=tubercle for the attachment of the *M. tibialis cranialis*, II-IV, metatarsals II-IV. Scale = 1cm.

S. australis indicates that this species was capable of perching.

Neuquenornis volans
Chiappe & Calvo, 1994

MATERIAL EXAMINED. HOLOTYPE: MUCPv-142 (Fig. 10), fairly complete skeleton preserving the caudal portion of the skull, elements of the wing

and shoulder, portions of the hind limb and a few thoracic vertebrae (Chiappe & Calvo, 1994). REFERRED SPECIMEN: MACN-RN-977, distal end of humerus.

LOCALITY AND HORIZON. MUCPv-142 comes from the city of Neuquén, Province of Neuquén. MACN-RN-977 was found at Puesto Tripailao, approximately 30km southwest of General Roca, Province of Río Negro, Argentina. Río Colorado Formation, Bajo de la

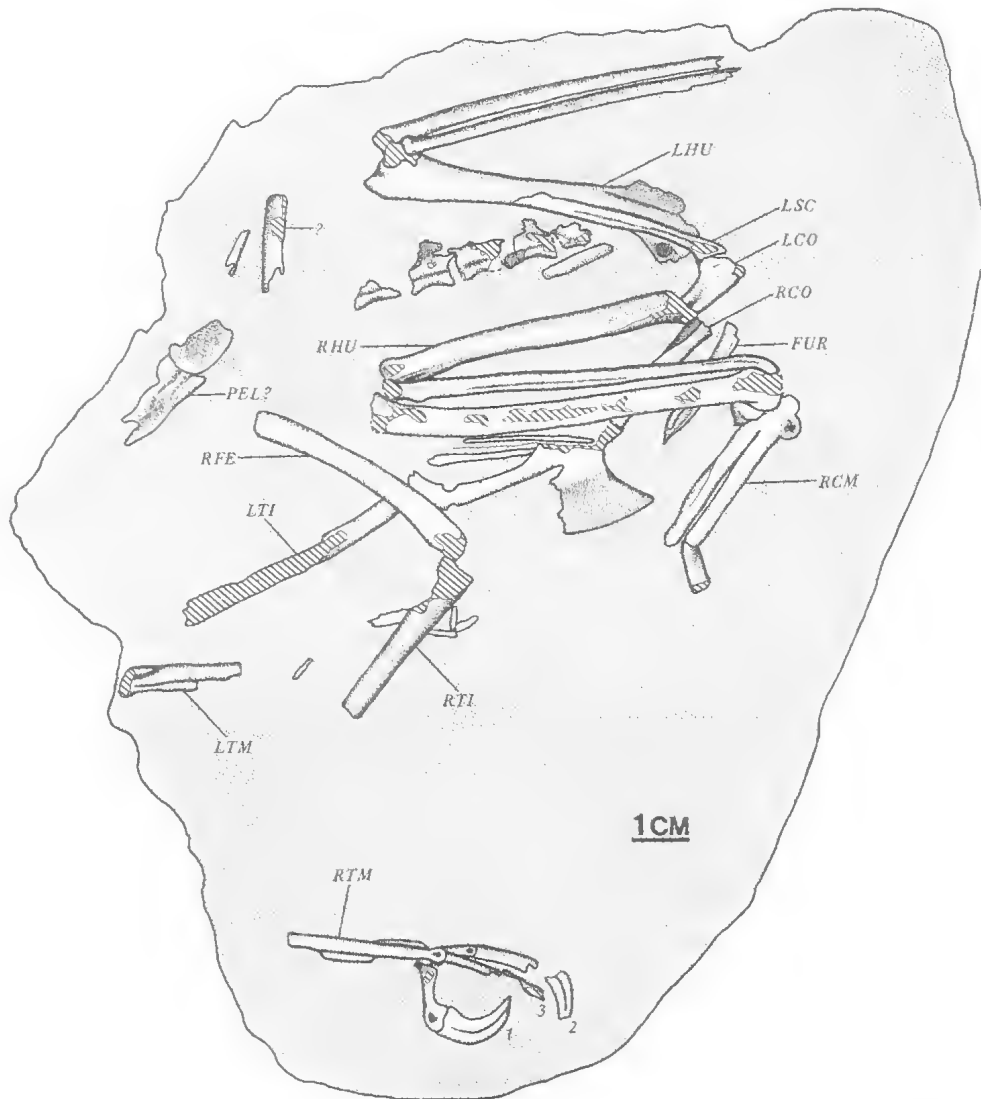


FIG. 10. *Neuquenornis volans* (MUCPv-142) from the Coniacian-Santonian Río Colorado Formation at the city of Neuquén, Province of Neuquén, Argentina (after Chiappe & Calvo, 1994). FUR=furcula, LCO=left coracoid, LHU=left humerus, LSC=left scapula, LTI=left tibiotarsus, LTM=left tarsometatarsus, PEL?=pelvis, RCM=right carpometacarpus, RCO=right coracoid, RFE=right femur, RHU=right humerus, RTI=right tibiotarsus, RTM=right tarsometatarsus.

Carpa Member, Late Cretaceous (Coniacian-Santonian; Chiappe & Calvo, 1994).

REMARKS. *Neuquenornis volans*, was a falcon-sized, active flyer whose enantiornithine affinity is supported by numerous synapomorphies in the thoracic limb (e.g., distal end of humerus cranio-caudally compressed) and girdle (e.g., coracoid with a convex lateral margin and a wide triangular fossa on its dorsal surface), pelvic limb (e.g.,

well-developed posterior trochanter of femur) and vertebral column (e.g., lateral grooves on thoracic centra) [see Chiappe & Calvo (1994) for a complete list of characters] (Fig. 10). The pedal anatomy indicates that *N. volans* is a member of the Avisauridae (Chiappe, 1993) and like *Soroavisaurus australis*, was capable of perching (Chiappe & Calvo, 1994). Specimen MACN-RN-977, although fragmentary, is identical in

size and morphology to the holotype of *Neuquenornis volans*.

ORNITHURAE Haeckel, 1866

MATERIAL EXAMINED. PVL-4730, a proximal half of a tibiotarsus (Powell, 1987). PVL-4731, portions of humerus, ulna, radius, carpometacarpus, and the proximal phalanx of the major digit (Fig. 5).

LOCALITY AND HORIZON. Salitral Moreno, 20km south of General Roca, Province of Rio Negro, Argentina. Allen Formation, Late Cretaceous (Maastrichtian; Powell, 1987).

REMARKS. These two specimens were found in the same quarry (Powell, pers. comm.). PVL-4730 exhibits two well-developed cnemial crests, typical of ornithurine birds (Figs 5A, B). PVL-4731 is significantly larger than PVL-4730 and, although these specimens have not been studied in detail, it probably represents a different species (Fig. 5C-E). The presence of a well-projected, pointed metacarpal process of the carpometacarpus (Fig. 5E) and a cranio-caudally expanded proximal phalanx of the major digit both support the allocation of PVL-4731 to the Ornithurae.

The fossiliferous beds of the Allen Formation at Salitral Moreno have provided a variety of dinosaurian remains including hadrosaurids (Powell, 1987), titanosaurid sauropods (Salgado & Coria, 1993), non-avian theropods (Coria, pers. comm.) and turtles (Salgado & Coria, 1993).

NEORNITHES Gadow, 1893 GAVIIDAE Allen, 1897

Neogaeornis wetzeli Lambrecht, 1929

MATERIAL EXAMINED. HOLOTYPE: GPMK-123, a right tarsometatarsus (Lambrecht, 1929).

LOCALITY AND HORIZON. West end of Bahía San Vicente, Province of Concepción, Chile. Quiriquina Formation, Late Cretaceous (Campanian-Maastrichtian; Biró Bagóczy, 1982).

REMARKS. Lambrecht (1929) considered *Neogaeornis wetzeli* as a hesperornithiform, a group of Cretaceous marine foot-propelled divers mostly known from North American beds (Olson, 1985; Chiappe, 1995a). Brodkorb (1963b) remarked on the affinity of this species to the hesperornithiform *Baptornis advenus*, including both in the Baptornithidae, in which he was followed by Martin & Tate (1976). The hesperornithiform relationship of *N. wetzeli*, however, was recently challenged by Olson (1992). After

repreparing the specimen, Olson (1992) regarded it as a loon and placed it within the foot-propelled, modern Gaviidae.

The Quiriquina Formation has afforded a great variety of invertebrates, fishes and reptiles (Biró-Bagóczy, 1982). The depositional environment of the Quiriquina Formation appears to have been a tidal plain (Biró-Bagóczy, 1982).

ANTARCTICA

AVES Linnaeus, 1758 METORNITHES Perle et al., 1993 ORNITHOTHORACES Chiappe, 1995 ORNITHURAE Haeckel, 1866 NEORNITHES Gadow, 1893 GAVIIDAE Allen, 1897

MATERIAL EXAMINED. A single specimen preserving parts of the skull, limbs, and a few cervical vertebrae (Chatterjee, 1989).

LOCALITY AND HORIZON. Marambio (Seymour) Island, Antarctic Peninsula. López de Bertodano Formation, Late Cretaceous (Campanian-Maastrichtian; Medina et al., 1989).

REMARKS. The first report of an Antarctic Cretaceous bird was given by Chatterjee (1989), who reported a loon-like bird from the Campanian-Maastrichtian López de Bertodano Formation of Marambio (Seymour) Island. Chatterjee's (1989) allocation of this fossil within the modern gaviiforms was corroborated by Olson (1992). This specimen represents the most southern occurrence of gaviiforms and along with *Neogaeornis wetzeli* (Lambrecht, 1929; see above) the oldest known loon.

The López de Bertodano Formation is primarily composed of marine medium-grained to silty sandstones (Zinsmeister, 1982; Medina et al., 1989), enclosing a diverse assemblage of microorganisms (Martinez Machiavello, 1987), plants (Askin, 1990) and invertebrates (Zinsmeister, 1982), along with fishes (Grande & Chatterjee, 1987), plesiosaurs (Gasparini et al., 1984) and mosasaurs (Gasparini & del Valle, 1984) among vertebrates. Medina et al. (1989) have summarised the paleoenvironment of this unit as ranging from an offshore marine shelf to near shore facies, including intertidal plains and deltaic environments.

PRESBYORNITHIDAE Wetmore, 1926

MATERIAL EXAMINED. MLP 93-1-3-1 and MLP 93-1-3-2, partial skeletons, apparently conspecific (Noricga & Tambussi, 1995).

LOCALITY AND HORIZON. Cape Lamb, Vega Island, Antarctic Peninsula. Cape Lamb strata, correlated to the López de Bertodano Formation (Unit B), Late Cretaceous (Campanian-Maastrichtian; Medina et al., 1989).

REMARKS. MLP 93-1-3-1 was briefly described by Noriega & Tambussi (1995). These authors regarded it as a member of the anseriforms Presbyornithidae (Ericson, 1992), an extinct group of Paleogene wading birds (Olson, 1985) previously represented in the southern continents by the Eocene *Telmabates* from Patagonia (Howard, 1955). If this interpretation is correct, these new findings expand the record of presbyornithids to the Cretaceous.

The marine deposits from where these fossils were recovered belong to the Maastrichtian section of the Late Cretaceous Cape Lamb strata (Zinsmeister, pers. comm.). These beds have been correlated to those of the López de Bertodano Formation at Marambio (Seymour) Island, although regarded as more marginal deposits within the same basin (Pirrie et al., 1991). The associated fauna primarily includes ammonites, gastropods, fishes and plesiosaurs (Zinsmeister, pers. comm.). The fact that these birds were found in marine deposits does not necessarily mean that they were oceanic birds, although it suggests that at least they inhabited marine littoral environments.

AFRICA

AVES Linnaeus, 1758

MATERIAL EXAMINED. Several footprints (Figs 4B, C, D) of unknown repository (Lockley et al., 1992).

LOCALITY AND HORIZON. 16km east of Agadir, Morocco (Ambroggi & Lapparent, 1954). Calcareous Maastrichtian beds (no formational name is given), Late Cretaceous.

REMARKS. Ambroggi & Lapparent (1954) regarded as avian a series of small tridactyl footprints (Figs 4B, C, D), about 3cm long, associated with other footprints of non-avian dinosaurs and lizards. The bird tracks were briefly described and poorly illustrated. One of them (Fig. 4D) was interpreted as having been made by a semi-palmate bird.

METORNITHES Perle et al., 1993

MATERIAL EXAMINED. Hind limb elements of two con-specific specimens (Krause, pers. comm.).

LOCALITY AND HORIZON. Near the village of Berivotra, Mahajanga Basin, northwestern Madagascar. Maevarano Formation, Late Cretaceous (Campanian; Krause et al., 1994).

REMARKS. The specimens belong to a new, undescribed taxon. Retention of several plesiomorphic characters (e.g., incompletely fused tibiotarsus and tarsometatarsus) suggest that this is a very primitive bird, although its phylogenetic placement remains to be analysed. This finding is extremely important because these specimens not only represent the first Mesozoic African bird known by skeletal evidence but also the first pre-Late Pleistocene avian from Madagascar.

The fossiliferous section of the Maevarano Formation consists of fluvial white sandstones. The poorly known Late Cretaceous fossil record of Madagascar has become substantially improved with the recent discovery of an ensemble of vertebrates from the Maevarano Formation that, in addition to the above mentioned birds, includes fishes, frogs, turtles, lizards, snakes, crocodiles, dinosaurs and mammals (Krause et al., 1994, in press).

DISCUSSION

In spite of a recent plethora of new findings, the Gondwanan record of Mesozoic birds is still very limited and restricted to the Cretaceous. This record is most diverse and extensive in South America, where birds are known from the Aptian to the Maastrichtian and from many localities. Within Australasia it is limited to the Early Cretaceous (Aptian-Albian) of Australia and in Antarctica it is restricted to the latest Cretaceous (Maastrichtian). Likewise, in Africa only a few footprints and a recently discovered new taxon from the Late Cretaceous of Morocco (Maastrichtian) and Madagascar (Campanian), respectively, stand as evidence of presence of Mesozoic birds in this continent.

Although the record is limited, the Mesozoic birds from Gondwana have contributed significantly to the growth of knowledge on early avian evolution. Taxa such as the *Enantiornithes* and *Patagopteryx deferrariisi* were among the first to provide evidence about the series of transformations which occurred between the primitive morphology of *Archaeopteryx lithographica* and that of more derived birds such as *Hesperornithiformes* and *Ichthyornithiformes* (Walker, 1981; Chiappe, 1992a, 1995a, b, 1996; Chiappe & Calvo, 1994). More recently, the histological

studies carried out on the bones of *Enantiornithes* and *P. deferrariisi* led to the first inferences on the rate of growth and related physiology of basal birds derived from reliable evidence (Chinsamy et al., 1994, 1995).

Using the Gondwanan record of Mesozoic birds for large scale paleobiogeographic analysis (e.g., Bonaparte, 1986, 1991; Chiappe, 1991; Noriega & Tambussi, 1995) is considered unreliable on the basis of the still insufficient evidence. For example, a Gondwanan origin of the *Enantiornithes* was claimed by Bonaparte (1986, 1991) on the basis of assumptions such as their 'oldest' record and their 'high' taxonomic diversity in South America [see Humphries & Parenti (1986) for a discussion of these theoretical issues]. This idea, however, has been shown to be an erroneous generalization based on an inadequate record. At present an abundant diversity of enantiornithine birds is known worldwide during the Cretaceous, and their oldest record to date is not in Gondwanan continents but in Europe and Asia (Chiappe & Calvo, 1994; Chiappe, 1995a; Sanz et al. 1995).

A general look at the Mesozoic record of birds from Gondwana reflects a broad, although punctuated, spectrum of geographic distributions, habitats and modes of life. During the Cretaceous, Gondwanan birds occupied a large latitudinal range, from near the equator to close to the Southern pole. These fossils have been recovered primarily from inland environments, although birds probably inhabited marine realms and seashores as well. The paleoenvironmental conditions of the localities in which Mesozoic Gondwanan birds were found range from warm and arid to near-freezing, at least during winter. A variety of modes of life have been inferred from their anatomy, such as flightless cursorials to foot-propelled divers, waders and perching active fliers.

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